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REVIEW ARTICLE

Urban-rural gradients: how landscape changes drive adaptive evolution of plant competitive traits

Yuya Fukano[1,3] · **Kei Uchida**[1] · **Yuuya Tachiki**[2]

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Abstract

The role of competition in local adaptation and the associated traits underlying adaptation remain unclear. One reason for the lack of evidence may be that plant-plant competition is ubiquitous in natural environments; thus, local adaptation to different levels of competition is difficult to test. Comparison between urban and rural habitats is suitable for examining the evolutionary impacts of competition because these habitats share several plant species, but differ greatly in plant density and their resulting degree of competition. Here, using methods of landscape ecology, we propose a landscape evolutionary ecological approach—a simple analytical framework—to investigate how landscape changes in urban–rural gradients drive the local adaptation of competitive traits. We demonstrated adaptive divergence of competitive traits (i.e. growth habits) between urban and rural populations in two Poaceae plants (*Digitaria ciliaris* and *Eleusine indica*) and summarised the experimental procedure to examine local adaptation to different levels of competitive environments. Landscape change due to urbanisation provides an opportunity to understand the drivers and constraints of the evolution of plant competitive traits. Our analytical framework will be useful for integrating research on urban evolution conducted in different countries and regions.

Keywords Digitaria ciliaris · Eleusine indica · Eco-evolutionary feedback · Convergent evolution · Urbanisation · Landscape ecology · GIS

✉ Yuya Fukano
yuya.fukano@gmail.com

[1] Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan

[2] Department of Biological Sciences, Tokyo Metropolitan University, Tokyo, Japan

[3] Graduate School of Horticulture, China University, Chiba, Japan

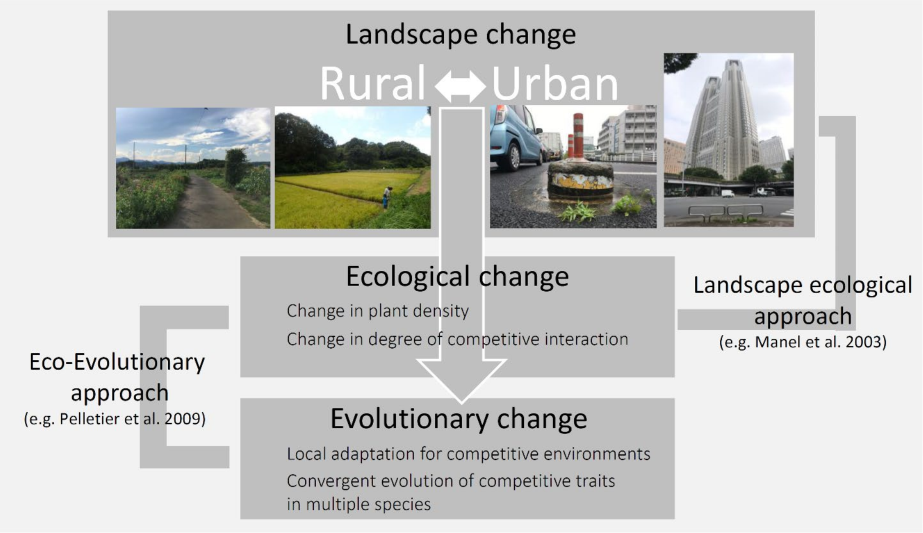


Fig. 1 The conceptual framework of this paper. First, we discuss how reduced competitive interaction in urban habitats leads to the evolution of reduced competitive ability and drives adaptive trait divergence in competitive traits (left side). Second, we propose a new analytical framework to examine how landscape changes due to urbanisation influence local adaptive evolution and landscape-level trait variation (right side)

Introduction

In plant communities, interspecific and intraspecific competition play a major ecological role in determining plant fitness, population dynamics, community structures, and ecosystem functions (Grime 1973; Fowler 1986; Hautier et al. 2009). However, compared with the ecological roles of competition, trait evolution in response to competition has not received much attention (Arthur 1982; Aarssen 1985; Cahill 2013; Aschehoug et al. 2016; Hart et al. 2019). Many studies have focused on plant traits that correlate with competitive ability, such as plant size (Grime 1974; Westoby 1998; Keddy et al. 2002). Several reports in plants of character displacement for traits related to resource acquisition and seedling growth (Veech et al. 2000; Beans 2014) suggest that competition is an important factor in plant trait evolution. However, little is known about how selection pressure due to competition drives local adaptation and the specific competitive traits that are selected. This paucity of studies is surprising, given that the evolutionary influences of other types of ecological interactions (e.g. abiotic conditions, herbivory, and pollination) on local adaptation and trait evolution have been well studied (Cheplick, 2015; Kawecki and Ebert 2004; Thompson, 2005; Wu, Bradshaw, & Thurman, 1975).

The landscape gradient between urban and rural environments provides suitable systems to examine the evolutionary impacts of competition on local adaptation and competitive traits for several reasons (Fig. 1). There are major differences in plant density, and thus, the degree of competition between urban and rural plant habitats (Williams et al. 2005; Kong and Nakagoshi 2006; Jiang et al. 2015). Farmlands in rural habitats provide suitable soil and water conditions for plant growth, causing plants in and around a crop field to grow at high density and experience strong competition. Although herbicides usually control weeds within farmland, a large area around farmland maintains high densities of numerous plant species (Marshall 2004; Petit et al. 2011). In contrast, the soil environment in urban areas varies widely, from impervious surfaces with little soil or vegetation to flowerbeds with nutrient-rich soil (Li et al. 2013; Mao et al. 2014). The impervious surfaces, which cover a large part of the urban habitats, harbour gaps with low amounts of nutrient-poor soil (e.g. roadside). These conditions in urban habitats cause plants to grow at low densities and experience weak above-ground competition. Weak above-ground competition in urban habitats promotes trait evolution via two evolutionary processes: relaxed selection and natural selection. Relaxed selection is termed as the environmental change that eliminates or weakens a source of selection that was formerly important for the maintenance of a particular trait (Lahti et al. 2009). Given that competitive traits can be defined as having evolved as a consequence of the competition for certain resources, these would benefit individual plants growing in strongly competitive environments. In contrast, these traits would impose fitness costs on the plants growing in the absence of competition or in weakly competitive environments (Kawecki and Ebert 2004; Chaney and Baucom 2014; Fukano et al. 2020). In urban environments, especially where low plant density and light competition are weak, such as small gaps in paved roads, relaxed selection will cause plants to lose competitive traits. If there are trade-offs between the amounts of resources for competition-related traits and that for growth and reproduction (cost of the competitive traits), natural selection, rather than relaxed selection, will favour genotypes that invest their resources into growth and reproduction by decreasing the resource for the competition. The types of traits that have a trade-off relationship with competitive traits might depend on the growth habits of the focal species, the competitive trait, and the growing conditions. For example, if the production of allelopathic compounds, which consumes large amounts of photosynthates, is deemed a competitive trait, assimilation efficiency (i.e., growth rate) will be reduced. Furthermore, if erect growth form is considered a competitive trait (Fukano et al. 2020), plant height is also a competitive trait, although its cost would appear as a reduction in photosynthetic efficiency (projected leaf area) under low plant density. Besides the advantage of contrasting selection pressures on competition-related traits, the urban–rural comparison has the advantage that these environments share a range of herbaceous species (Levenson 1997). The overlap in species composition among habitats allows us to directly test their local adaptation to high or low level of competition by comparing the urban and farmland populations.

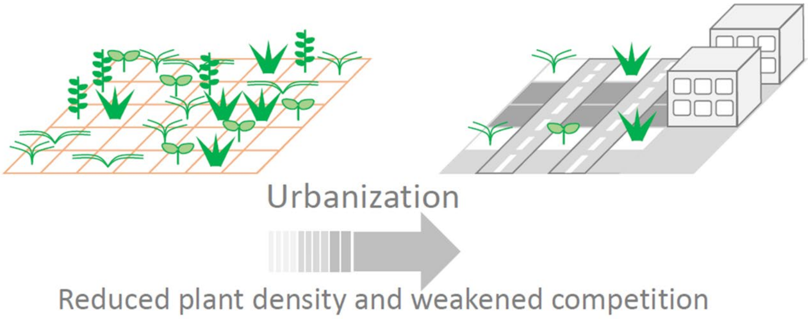
In recent years, rapid adaptive evolution in urban and rural gradients has received a lot of attention (Johnson and Munshi-South 2017; Santangelo et al. 2018; Rivkin et al. 2019; Fukano et al. 2020; Lambert et al. 2020a). Since the urban landscape is a recently emerged habitat, focusing on local adaptation in urban habitats enables us to obtain a detailed understanding of the pace, process, and constraint of adaptive evolution. For example, we can examine the environmental changes due to urbanisation which impose directional selection (Start et al. 2018; Puckett et al. 2020) and drive adaptive evolution (Brans et al. 2017; Halfwerk et al. 2019), and how trait differentiation is shaped by local adaptation in the presence of gene flow from neighbouring populations (Johnson et al. 2018; Theodorou et al. 2018). Our framework highlights the suitability of comparing urban and rural populations to understand the nature of adaptive evolution. Numerous studies have focused on various types of selective agents and reported divergent selection between urban and rural populations, phenotypic changes, and adaptive evolution (Johnson and Munshi-South 2017; Santangelo et al. 2018; Rivkin et al. 2019; Lambert et al. 2020b). Despite the apparent decline in plant density in some local environments in urban habitats, changes in competitive interactions, as selective agents in urban habitats, have received little attention.

As both urbanization and conversion to farmland are large-scale changes in landscape elements and structures, rapid adaptation in urban–rural gradients can be understood in terms of the evolutionary impacts of landscape change. Determining how landscape-level geographical and environmental factors drive adaptive genetic changes is a major challenge in evolutionary biology (Lowry 2010). Therefore, examining rapid adaptive evolution in urban and rural gradients is an opportunity to bridge landscape and evolutionary ecology. Several recent pioneering studies of urban evolution have examined the influence of landscape-derived environmental factors on trait evolution (Thompson et al. 2016; Santangelo et al. 2022). However, well-developed analytical methods applied in landscape ecology were not incorporated into the study of trait evolution in these studies. In landscape ecology, spatial statistical modelling, including geographic information system (GIS) analysis, have been widely used to examine spatial autocorrelation among populations and communities, and to estimate the geographical distribution of specific species. Using these techniques in landscape analysis, we can gain a deeper understanding of how changes in landscape elements due to urbanization drive the adaptive evolution of plant traits, including competitive traits.

This review is organized as follows. First (Sect. 2), we explain the evolutionary scenario of reduced competitive ability in urban plant populations. Second (Sect. 3), using landscape ecological methods, we propose a novel analytical approach to investigate how landscape changes due to urbanisation drive the local adaptation of competitive traits. In this section, we summarise the experimental procedure to examine local adaptation to changes in competition and identify its associated traits by differentiating it from other urbanisation-derived traits. Then, we introduce the usefulness of urban-rural comparison for evolutionary research of competitive traits by presenting the experimental results of convergent evolution of competitive traits in two Poaceae annual plants, *Digitaria ciliaris*(Fukano et al. 2020) and *Eleusine indica* (Fukano, unpublished data). Furthermore, we explain the analytical procedure to integrate competitive trait values obtained from evolutionary ecological experiments into landscape analyses to understand how local landscape elements and size affect the local adaptation of competitive traits. Finally (Sect. 4), we suggest some future research, with an emphasis on eco-evolutionary feedback(Pelletier et al. 2009; Rivkin et al. 2019) of competitive traits.

Competitive trait divergence in urban-rural gradients

It can be predicted that reduced plant density and weak plant-plant competition in urban habitats will lead to reduced competitive ability in these populations by both relaxed selection and directional selection (Bossdorf et al. 2004; Chaney and Baucom 2014Fig. 2). For example, potential competitive traits such as height, above-ground growth form, root growth pattern, and allelopathy can be rapidly modified by relaxed selection in urban populations where competition is weaker than in natural or farmland populations (Jiang et al. 2015; Kong and Nakagoshi 2006; Williams et al. 2005). Traits related to high growth rate and large biomass would contribute to both competitive ability and growth and reproduction.



Predicted change	Potential associated traits	Key references
Reduced competitive ability	Growth form, leaf shape, root morphology and behavior, allelopathy	Bossdorf et al. (2004), Chaney & Baucom (2014), Fukano et al. (2020)
Increased growth rate under weak competitive environment	Growth form, leaf shape, root morphology and behavior, photosynthesis rate	Miller (1995) Fukano et al. (2020)
Increased allocation to reproduction	Allocation to flowers and seeds, timing of reproduction, seed size	Donald (1962), Miller (1995), Zhang et al. (1999)

Fig. 2 The scenario for the process of adaptive evolution under low plant density and weak competition in urban habitats. Weak competition in urban habitats gives rise to new selective pressures and may lead to rapid changes in certain competitive traits

Conversely, increased allelopathy and changes in the above-ground growth form would be the competitive traits that have trade-off relationships with growth and reproduction. The reduced competitive interaction due to urbanization may trigger evolution in these traits, while the evolution in the latter traits may be more rapid compared with the former traits (Fig. 2). This is because competitive traits will be lost more quickly through natural selection if there are trade-offs between the amounts of resources for competition-related traits and other traits (e.g., growth and reproduction), which then increases growth and reproductive traits (Donald 1968; Miller 1995; Zhang et al. 1999). In this situation, urban populations may evolve traits that maximise growth and reproductive performance under weak competition at the expense of competitive ability. This would result in the adaptive divergence of competitive traits between urban and farmland populations (Fukano et al. 2020). Such an evolutionary scenario was originally proposed to explain the success of some invasive plants (the evolution of the reduced competitive ability hypothesis (Bossdorf et al. 2004) modified from the evolution of increased competitive ability hypothesis (Blossey and Nötzold 1995)), but it has received little attention or testing (Atwood and Meyerson 2011). We propose that such evolution is common in urban plant populations (Fig. 2).

In contrast, rural habitats have relatively higher nutrient and water contents than urban areas (Williams et al. 2005; Kong and Nakagoshi 2006), although the magnitude of evapotranspiration in urban areas varies globally (Mazrooei et al. 2021). As a result, many plants other than crops grow in and around farmlands at a high density and are recognised as weeds (Marshall 2004; Petit et al. 2011). While the amount of nutrient input must be higher in rural than in urban habitats, the amount of light resources should be almost the same in urban and rural habitats. Thus, above-ground competition will increase in rural habitats, as nutrient inputs increase plant growth and density. Increased plant density and strong plant–plant competition in rural habitats may enhance the competitive ability for aboveground competition via directional selection (Miller 1995; Cahill 2013).

Landscape evolutionary ecology for urban evolution

Urbanisation creates changes in landscape elements and structures. Thus, rapid local adaptation of competitive traits in urban–rural gradients can be examined in terms of landscape change. A major challenge in evolutionary biology is determining how landscape-level geographical and environmental factors drive adaptive genetic changes (Lowry 2010). Studies on urban evolution are suitable systems for linking landscape and evolutionary ecology (Alberti et al. 2020; Des Roches et al. 2020). Landscape ecological and genetic studies have revealed that changes in landscape elements and patterns due to urbanisation can dramatically change species distribution, migration, gene flow, and genetic structure (Manel et al. 2003; Turner 2005; Manel and Holderegger 2013). Using methods of landscape ecology [e.g. spatial statistical modelling and geographic information system (GIS)], we can assess how changes in landscape elements due to urbanisation drive the adaptive evolution of living organisms. Landscape genetics, which combines landscape ecology with population genetics, focusses on genetic variations in neutral loci to determine the effects of landscape elements on migration barriers and population genetic connectivity of individual organisms (Manel et al. 2003; Manel and Holderegger 2013). However, our concept of 'landscape evolutionary ecology' focuses on spatial variations in phenotypic values, measured in common garden settings, to determine the effect of landscape elements on the process and scale of trait adaptation (Fig. 3). Here, we introduce a landscape evolutionary ecological approach to understand how changes in landscape elements can explain local adaptation by presenting the case study of rapid adaptive divergence in competitive traits along urban–rural gradients.

We provide a three-step landscape evolutionary ecological approach (Fig. 3). The first step involves evolutionary ecological experiments to examine local adaptation and competitive trait divergence (Sect. 3.1, 3.2, and 3.3). The second step involves the collection of environmental and geographical data around the sampling location using GIS (Sect. 3.4). Finally, the third step involves the integration of evolutionary and landscape ecology to understand the local adaptation of competitive traits in terms of landscape elements and the surrounding environment of the local population (3.5).

Experimental procedures to test competitive trait divergence

While competition intensity may be one of the most obvious environmental changes caused by urbanisation, various other biotic and abiotic variables differ between urban and rural areas (Miles et al. 2019; Song et al. 2019; Hou et al. 2020). Hence, several procedures are required to differentiate adaptation to competition from other evolutionary forces. We summarise the following procedures to examine how competition-driven selection promotes local adaptation in urban and rural (farmland) populations and identify competitive traits associated with adaptation (Fig. 3). It should be noted, however, that this procedure focuses on the adaptations in intraspecific competition, and it is conceivable that traits considered

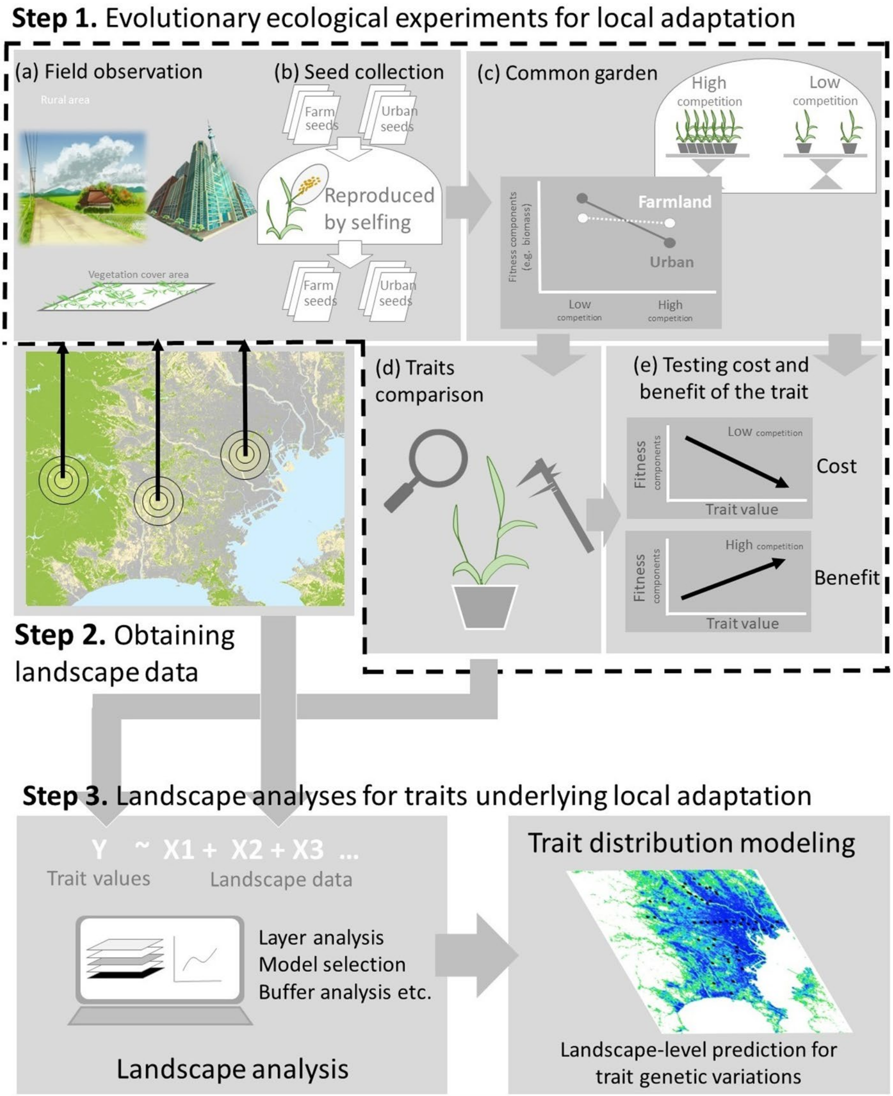


Fig. 3 The conceptual framework of the landscape evolutionary ecological approach. The first step involves evolutionary ecological experiments to examine local adaptation and competitive trait divergence. This step explains the experimental procedures to test the adaptive divergence of competitive traits between urban and rural (farmland) populations and identify the associated traits. This step consists of five procedures: (a) field observation of urban and farmland areas, (b) seed collection from each population, (c) fitness measurement in common garden, (d) trait comparison, and (e) testing cost and benefit of the trait. The second step involves the collection of environmental and geographical data around the sampling location using GIS. Finally, the third step involves the integration of trait data obtained from the evolutionary ecological experiments and landscape data obtained using GIS. Several landscape analytical tools can be used to understand how local landscape elements and size affect the local adaptation of competitive traits and to predict landscape-level variations in the competitive traits

adaptive with respect to interspecific competition may differ from those considered adaptive under conditions of intraspecific competition.

a, Field observation of the level of competition between urban and rural populations.

By setting quadrats to record the vegetation cover and species composition around the target plant, the degree of competitive interaction between urban and rural habitats can be compared. Ideally, these measurements should be conducted at the end of the vegetative growth period when light competition is most intense. However, this measurement only reflects above-ground competition. To quantify below-ground competition, additional measurements, such as root volume, are essential.

b. Collection of seeds from urban and rural populations.

Seeds from urban and rural populations can be collected. All lineages would be multiplied by selfing in a greenhouse under the same environmental conditions to reduce parental effects for the common garden experiment. The collected seeds can be used for further experiments.

c. Measurement of fitness under strong and weak competitive conditions in a common garden or reciprocal transplant experiment.

If rural and urban populations locally adapt to their competitive environments, the former would achieve a higher growth rate and fitness than the latter under strong competition but the latter would achieve a higher growth rate and fitness than the former under weak competition. Reciprocal transplant experiments can directly test local adaptation to urban and rural habitats. However, because the biotic and abiotic conditions differ between urban and rural areas, transplant experiments alone cannot identify the precise selection pressure that drives local adaptation. Whether competitive conditions can drive local adaptation can be tested by growing plants in a common garden, where only competitive conditions are altered. For instance, growing individual plants in containers and manipulating the distance between them would only change the above-ground competitive conditions.

d. Trait comparison.

To identify the traits associated with local adaptation, various traits likely to be involved in plant competition can be compared between rural and urban populations. For instance, plant height, growth form, and leaf area index are the candidate competitive traits (Fig. 2).

e. Cost and benefit of testing competitive traits.

If a trait evolves as a result of competition, it would benefit the individual plants growing under strongly competitive environments; however, this trait would impose a fitness cost on the plants growing in the absence of competition or under weakly competitive environments (Kawecki and Ebert 2004; Chaney and Baucom 2014; Fukano et al. 2020). Even if we can observe trait differences between urban and farmland populations through trait comparison (d), we do not know what ecological factors may have caused these differences. For example, plant height is related not only to above-ground competition but also to pollination and seed dispersal. This procedure allows us to estimate the ecological factors acting as selection pressures that produce differences in traits. Examination of such a trade-off is key to understanding the evolutionary dynamics of competitive traits in urban and rural habitats. Traits that are positively correlated with fitness components under strongly competitive conditions (fitness benefit) and those negatively correlated with fitness components under weakly competitive conditions (fitness cost) must be identified. For example, in the case of *Digitaria ciliaris*, the height/width ratio of above-ground shoots is positively correlated with individual biomass in the presence of above-ground competition. In contrast, this trait was negatively correlated with biomass in the absence of above-ground competition

(Fukano et al. 2020). Thus, the height/width ratio is thought to be an essential trait for the evolution of competitive ability. Similarly, in *Ipomoea purpurea*, relative growth rate can be considered as a trait associated with tolerance to competition, and late flowering can be considered the cost of the tolerance (Chaney and Baucom 2014).

Evidence of competitive trait divergence

We conducted a study using the above framework. We showed that the urban and rural populations of *Digitaria ciliaris*, a common weed in both habitats, are locally adapted to different competitive environments. The key local adaptive traits are the height/width ratio and stem diameter (Fukano et al. 2020, Fig. 4a-c). Competitive traits here are viewed as traits related to local adaptation due to differences in plant-plant competition. Hence, it is necessary to demonstrate the benefits and costs of competitive traits. In strongly competitive environments, populations with a higher height/width ratio (i.e., farmland populations in rural habitats) were more tolerant of above-ground competition. In contrast, in weakly competitive environments, individuals with a higher height/width ratio achieved lower growth rates. This trade-off indicates that the height/width ratio is a key competitive trait in the urban and rural populations (Fukano et al. 2020).

Previous studies on the urban evolution of competitive traits have focused only on growth habit as a competitive trait (Fukano et al. 2020), although various traits are expected to evolve in response to changes in competition. For instance, above-ground traits, such as leaf width and length, photosynthetic efficiency, and growth rate, are tightly linked to competitive ability (Baker 1974; Keddy et al. 2002). In addition, competitive traits both above- and below-ground may differ between urban and rural populations (Zangaro et al. 2016; Semchenko et al. 2018). For example, above- and below-ground resource allocation may change depending on the relative importance of limited resources between light and soil nutrients. Suppose soil nutrients are a limiting resource in urban environments. In that case, urban populations can change their below-ground traits associated with competition for nutrients, such as root system size, root length, and proportion of branched roots. However, predicting the evolutionary consequences on trait differentiation between urban and rural habitats may be more difficult for below-ground competition than for above-ground competition. Because soil nutrients, moisture, and hardness markedly differ between urban and rural habitats (Li et al. 2013; Jiang et al. 2015), plants may evolve their root physiological and morphological traits in response to the physical environment of the soil, in addition to competitive interactions. In this context, the above experimental procedures may help examine how competition as a selection pressure drives below-ground trait evolution, distinguishing it from the other types of selection pressures. Elucidating rapid trait diversification in response to diverse soil physical environments between urban and rural habitats would offer vital insights into the adaptive evolution of below-ground traits in plants. However, such processes have never been tested.

Case study for convergent evolution of competitive trait

If urban–rural habitats impose a strong selection pressure on living organisms, adaptive trait divergence should be accomplished consistently in multiple species (i.e. convergent evolution). Convergent evolution provides some of the clearest evidence for adaptation

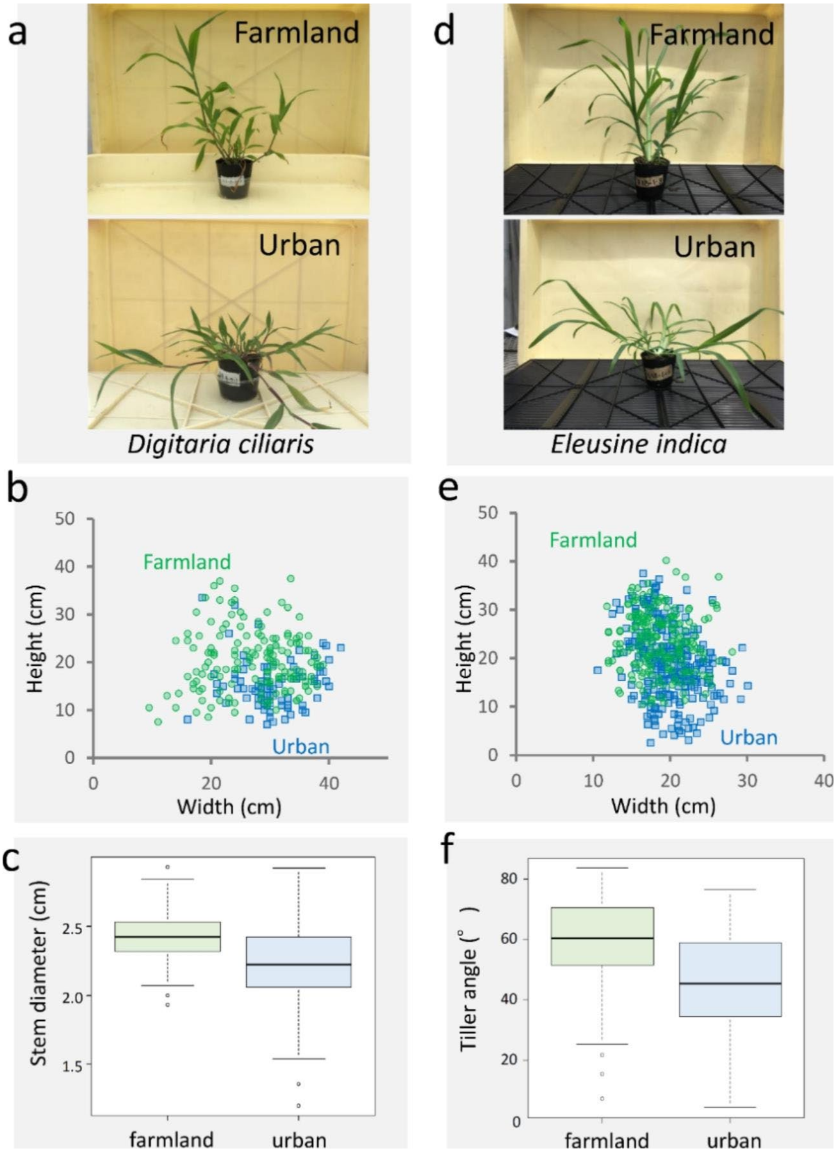


Fig. 4 Representative photographs of *Digitaria ciliaris* (a) and *Eleusine indica* (d) plants collected from rural (farmland) and urban habitats. The relationship between the height and width of *D. ciliaris* (b) and *E. indica* (e) from rural (green circles) and urban (blue squares) populations. Comparison of key traits associated with morphological differences in *D. ciliaris* (stem diameter) (c) and *E. indica* (tiller angle, main stem to the ground angle) (f) between urban and rural habitats

(Harvey and Pagel 1991; Losos 2011), and it also offers insights into the process and diversity of adaptive evolution. For instance, we can understand how various species with different physiological constraints adapt to the same selection regime. Convergent evolution in urban–rural habitats is of special interest to evolutionary ecologists because the earliest stages of convergent evolution are difficult to observe in wild and natural populations (Pascoal et al., 2014). To support our framework, we have extended the research conducted by Fukano et al. (2020) to include greater trait measurements and a second species, namely, *Eleusine indica*.

We collected seeds of *Eleusine indica* from 17 urban and 17 farmland populations and compared the plant traits between them (n=260 and 198 for urban and farmland, respectively), following a previous study (Fukano et al. 2020). *E. indica* is a common weed that grows sympatrically with *D. ciliaris* in both urban and rural habitats (Supporting Information 1). The common garden experiment demonstrated the phenotypic divergence of growth habits in *E. indica* populations, parallel to the case of *D. ciliaris*: plants from the farmland habitat had greater height, smaller width, and a larger height/width ratio than plants from the urban habitat (Fig. 4d and e). These results provide clear evidence of convergent evolution of competitive traits in urban and farmland habitats, suggesting that annual plants living in urban and farmland habitats are evolving in response to a strong disruptive selection pressure, and changes in the intensity of the competition lead to rapid trait evolution.

Interestingly, while the divergence pattern in overall growth habits was similar between *D. ciliaris* and *E. indica*, the physiological mechanism behind the morphological divergence may differ between the two species. *D. ciliaris* has a well-defined node on its stem, and the individuals with prostrate growth habit have narrower stems and expand horizontally, whereas individuals with erect growth habit have thicker stems and can extend vertically (Fig. 4c). In contrast, the stems of *E. indica* lack nodes, and their tiller angle (main stem to the ground angle) directly influences the morphological divergence between prostrate and erect growth habit (Fig. 4f). A similar pattern in morphological differentiation between urban and farmland populations in these two species indicates that plants can respond flexibly to the same selection regime due to anthropogenic environment, even with morphological and developmental constraints. The results imply that strong selection due to urbanisation induces rapid evolutionary changes in competitive traits of the entire plant communities; however, their associated traits may differ depending on the plant species. Prostrate growth habits are related to resistance to trampling and mowing stress (Völler, Bossdorf, Prati, & Auge, 2017; Warwick, 1980). However, these stresses might not be the primary drivers of the differentiation of height/width ratios between farmland and urban populations of *D. ciliaris* and *E. indica* because farmland populations might experience more trampling stress (e.g. due to agricultural machinery) and mowing stress than urban populations.

Environmental and geographical data

The second step is to collect environmental and geographical data for a specific radius around the sampling locations using GIS. Environmental data include temperature, precipitation, and solar radiation and geographical data include land use pattern and slope. Specific social variables derived from anthropogenic activity (such as the human footprint index, land price, and traffic level) may also be important for the analysis. If the GIS data that are expected to be relevant to the selection pressure of interest are obtained, the impact of spatial variations in environmental, geographical, and social factors on adaptive local evolution can be tested. For instance, Santangelo et al. (2020) demonstrated that the parallel urban–rural cline in the antiherbivore defensive traits of *Trifolium repens* is affected by local climatic conditions throughout eastern North America.

Integrating local adaptation into landscape analysis

The third step integrates local adaptation into landscape analysis. This analysis aimed to examine whether landscape elements were related to the researchers' traits of interest. Statistical analysis can be performed using trait values in a common garden as the response variable, and the landscape element data of each population, obtained via publicly available land-use mapping, such as the high-resolution land use and land cover map from JAXA (https://www.eorc.jaxa.jp/ALOS/a/en/index_e.htm) and Landsat data from NASA (https://landsat.gsfc.nasa.gov/data), as explanatory variables. Landscape element data on land use can be analysed directly as an explanatory variable or can be used to estimate environmental and geographical data in different regions (Sect. 3.4). For this analysis, an array of methods used in landscape ecology can be implemented (Manel et al. 2003; Manel and Holderegger 2013). For instance, buffer analysis can estimate the best predictive landscape size (i.e., the size of the landscape that best explains the spatial variation of adaptive traits), thereby explaining the observed spatial variation in the target traits based on the Akaike Information Criteria (AIC). Model selection based on AIC allows for estimating the combination of environmental and geographical variables and landscape size with the best predictive power to explain spatial variations in the local adaptation of the target traits. Finally, based on the best predictive model selected by AIC and large-scale environmental and geographical data, the landscape-level variations in the target traits can be estimated and depicted on a map.

Benefits of the landscape evolutionary ecological approach

The landscape evolutionary ecological approach will be of great benefit to the study of urban evolution. First, this approach can examine trait variation not only among urban and rural habitats but also within habitats. Numerous studies have reported phenotypic divergence between urban and rural habitats (Alberti et al., 2017; Rivkin et al. 2019; Santangelo et al. 2018). In addition, some studies have reported large variations even within urban and rural populations (Gorton et al. 2018). One of the major challenges of urban evolution is to explain the large variations within urban environments. Variations in landscape elements within urban and rural habitats can explain variations in traits. Second, while urban evolution has been examined in various cities around the world, the degree of urbanisation in each city varies across countries and regions (from European cities with sporadic green spaces and farmlands to highly urbanised Asian megacities with little greenery)(Schilthuizen 2019).

A standard scale for using landscape analysis via GIS will be helpful to unify the evolutionary findings across different cities and regions and to discuss the evolutionary impact of urbanisation on a global scale. Future comparative studies on various cities on a standard scale will elucidate the relationship between the degree of urbanisation, the speed of adaptive evolution, and the landscape elements that influence adaptive evolution. Third, various types of environmental data can be included in the model as explanatory variables for AIC-based model selection of target traits. For instance, increased temperature at the city centre (heat islands) have caused the evolution of increased heat tolerance in several animals (Brans et al. 2017; Campbell-Staton et al. 2020). Our proposed approach allows for the examination of not only the individual effects of landscape elements and physical environments but also their interactive effects on the evolutionary changes in urban organisms. In a previous section, we mentioned that the reduction in light resources due to urban buildings may be less pronounced than that due to vegetation in natural grasslands (Kjelgren 1995, Takagi & Gyokusen 2004). We can test this assumption by including the interaction between landscape elements and light resources into the model.

Fourth, our landscape evolutionary ecological approach may explain trait variations not only among populations but also within them. The phenotypic values of adaptive traits within populations may be affected not only by the selection pressure in local habitats but also by the phenotypic values of the neighbouring populations through migration and pollen dispersal. If the number of potential populations is limited and the phenotypic values of most of them can be measured, the effects of neighbouring populations can be estimated by applying techniques developed in landscape genetics. For example, an assignment test and parentage analysis may help estimate the occurrence of recent and current gene flow from the neighbouring populations (Holderegger and Wagner 2008). Fifth, the impact of the past and future land use on the phenotypic variations of adaptive traits can be evaluated. For instance, if future landscape changes can be predicted based on land use planning, the predictive model can forecast changes in the spatial patterns of trait evolution. Such predictions are crucial, particularly in studies in which the traits of interest are related to pest control and public health (Des Roches et al. 2020). Moreover, the impact of land use changes in the past due to urbanisation on the current status of spatial variation in adaptive traits can be examined (Epps and Keyghobadi 2015).

Finally, the framework of this approach can be applied to many types of natural and artificial ecosystems. This study focused on the urban-rural gradient as the contrast between plant density and competitive interactions. Similar types of plant density can be observed in the natural ecosystem, such as contrasts between habitats contaminated by heavy metals and those not contaminated and between habitats in the early and late successional stages. Adaptive divergence in competitive traits can be observed in these habitats. Our proposed framework combined with the aerial image of these habitats might clarify the impact of plant density and vegetation type on the evolution of competitive ability.

Conclusion and future remarks

In this short review, we demonstrated that urban-rural comparison is useful in understanding the adaptive nature of competitive traits in plants. Our example of convergent evolution of growth habits in *D. ciliaris* and *E. indica* demonstrated that competitive interactions drive plant trait diversification. In addition, we showed that the application of landscape approaches has the potential to accelerate the development of urban evolution research.

In future studies, urban-rural comparisons may greatly improve our understanding of the eco-evolutionary dynamics of competitive traits in plants. First, our case study of adaptive divergence of competitive traits in urban and farmland populations in *D. ciliaris* and *E. indica* suggests that many other plant species can also change their competitive traits in response to changes in plant density. Examining the adaptive divergence of competitive traits between urban and rural habitats in various plant species may help to identify the traits associated with competition and understand the role of phylogenetic and physiological constraints in competitive trait evolution. Second, the evolution of competitive traits may have a significant impact on the dynamics of intraspecific and interspecies competition

(Fukano et al. 2022). We examined trait evolution in response to changes in competitive environments (eco-to-evo); however, the evolution of competitive traits will have a significant impact on the consequences of competition (evo-to-eco). By using urban and farmland lineages and conducting competition experiments under laboratory and field conditions, we would be able to examine the eco-evolutionary dynamics between competitive traits and competitive interactions. Third, the evolution of competitive traits may affect weediness. In farmland, strong competition favours more erected phenotypes, and these phenotypes may have a greater negative impact on crop yield than the urban prostrate phenotype. Notably, *D. ciliaris* and *E. indica* have become problematic in croplands as noxious weeds around the world (Chauhan and Opeña 2012). In the future, it will be necessary to examine how the evolution of the increased competitive ability of weeds in farmland has a negative impact on crop yields.

Currently, this framework is designed to examine and predict how landscape elements affect the genetic variation of traits spatially (i.e., evolution in response to urbanization). Therefore, the plastic response of traits to landscape elements was not incorporated into the framework. In the future, the framework could be extended to include the effects of phenotypic plasticity. This would require measuring phenotypes in multiple environmental conditions derived from landscape differences and then quantifying the contribution of environmental variance, genetic variance, and the interaction of these. With an expanded framework, it may be possible to predict not only the spatial genetic variability of a trait but also the spatial variation of the trait value in different landscape growing conditions. To build better predictive models of local adaptation, several landscape elements and environmental factors that influence local adaptation need to be included in the model. Some databases, such as that of land use, precipitation, and temperature, are already available for many urban and rural locations. On the other hand, databases of sky openness and belowground biogeochemical components (e.g., nutrients), which may affect plant-plant competition, have not been well developed. In the future, it will be necessary to include these databases and develop techniques to monitor and estimate these environmental factors from satellite and aerial images.

Our proposed landscape evolutionary ecological approach allowed us to not only identify landscape or environmental factors influencing the local adaptation of competitive traits, but also to estimate their effective landscape size. Future applications of this approach to various studies of urban evolution will elucidate general patterns of how trait evolution is driven by anthropogenic landscapes or environmental changes due to urbanisation and the traits that are affected by landscape size. By combining landscape genomics, which investigates how landscape patterns influence genomic variation for adaptive evolution (Li et al. 2017; Rellstab, Gugerli, Eckert, Hancock, & Holderegger, 2015), we will be able to understand how landscape changes drive or inhibit adaptive trait evolution at the genomic level. Comparing the trait evolution between urban and rural habitats using these techniques may provide a bridge between evolutionary and landscape ecology.

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Authors' Contribution YF, KU, and YT developed the ideas and prepared the figures; YF drafted and coordinated the manuscript preparation; KU conducted GIS analysis; YF, KU, and YT contributed to writing all sections and revisions.

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Data Availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code Availability R code used in this study is available upon request from the corresponding author.

Declarations

Conflict of Interest We have no affiliations or involvement with any organisation or entity with any financial or non-financial interest in the subject matter or materials discussed in this manuscript.

Consent for Publication All authors consent to publication.

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